THE
AMERICAN NATURALIST

THE BOTANICAL SOCIETY OF AMERICA[1]

I. THE NATURE OF PHYSIOLOGICAL RESPONSE

BY THE LATE PROFESSOR CHARLES R. BARNES

UNIVERSITY OF CHICAGO

LIVING plants could hardly have been observed at all
without recognition of the fact that they are affected by
external conditions. These effects, when first observed,
were undoubtedly interpreted as mere conditions of liv-
ing, and our interpretation to-day has hardly gone be-
yond this. A moderate temperature, an adequate supply
of water, and the normal light are necessary for green
plants; and when these conditions are suitable the gen-
eral behavior of the plant is affected. All its processes
have a healthy *tone;* it flourishes; and the factors which
operate to produce this condition are declared to be *tonic.*
When the effects of external agents are studied more
closely, several peculiarities appear. Even these tonic
factors are seen frequently to produce quite limited
changes in behavior, though they may act simultane-
ously upon all parts of the body. Especially is this the
case when there is some sudden change in the intensity
or direction of these factors. Thus if the air tempera-
ture falls a few degrees on some spring day when the
crocuses are in bloom, the perianth segments promptly
curve inwards and close the flower. Or if the sunlight is

obscured by clouds, the dandelion heads are soon folded together by the straightening up of the involucral bracts. No other changes are visible, though others may be detected by appropriate means.

Again, external agents may act on only a limited region of the plant, in which case the obvious effects may be restricted to some special part, either that immediately acted upon or one at a greater or less distance from it. Thus if the cotyledon alone of a *Panicum* seedling be lighted from one side, the hypocotyl, 20 mm. or more away, instead of continuing its equal growth, may curve abruptly.

In these two cases of limited visible change, the phenomena are explained by asserting that the protoplasm is *irritable* and *responds* to an external change called a *stimulus*. In fact, there is an inclination, after endowing the protoplasm with such '' properties'' as ''irritability,'' ''automaticity'' and ''self-regulation,'' to be satisfied with the words and there make an end. Such a tendency, wide-spread in the prescientific days, undoubtedly springs from the wonder with which one confronts an uncomprehended intricate mechanism. It finds expression, for example, in a common saying about this or that industrial machine: ''It seems to have almost human intelligence.'' Of course no one supposes the machine really endowed with other than physical qualities, operating through the matter and the energy with which it is supplied. Yet the vitalism, which dominated the earlier years of physiology, even yet controls our speech and our thinking, and indeed lately shows signs of revival.

Vitalism, assuming living matter to be endowed with special powers, called vital in distinction from physical, is itself in part an expression of helplessness in the face of an uncomprehended mechanism, the living body, and in part an interpretation of nature in terms of our own consciousness. To seek explanation in that direction is to proceed from the simple to the complex; but the explanation of phenomena must be a process of analysis,

not of synthesis, and so of necessity proceeds in the other direction. We may not believe it possible to account for the behavior of living things by considering them as mechanisms whose actions are to be described in terms of matter and energy; and certainly it is not possible to do this now for any but the simplest actions. Yet it must not be forgotten that all the progress that has been made has been made in this direction; so that it commends itself to us both by the *a priori* and the inductive method.

The phenomena of response are probably the most complicated to be seen in the plant, and as yet we are far from being able to describe them completely in terms of physics and chemistry. I purpose only to present some suggestions on the nature of these phenomena, as a contribution toward the mechanistic conception of the plant, in the hope that this presentation may help to rid us of some of the subconscious vitalistic notions that are apt to cling so persistently about our thought and speech.

First let us consider the relation of the phenomena of response in living and non-living matter. To speak of response by non-living matter can occasion no surprise. Sachs, long ago, in his "Lectures on the Physiology of Plants," pointed out the fact that response is not peculiar to living things, citing as an example the crystals of the yellow iodide of mercury, which change their constitution and color when stimulated by various agents— a scratch sufficing to initiate a change which spreads gradually through the whole. Many other substances behave similarly. To explain such a change we predicate a state of metastable molecular equilibrium, the upsetting of which at one point incites a spreading disturbance, as a row of properly spaced blocks fall.

There is another sort of response in non-living matter, which is conditioned by external factors. In moist air many anhydrous salts and oxids unite with water, and in some cases in proportions differing with the amount of the vapor pressure. Thus, anhydrous copper sulfate, at a temperature of 50° C. with the vapor pressure gradually increasing from zero, would take up one molecule of

water and become the monohydrate as soon as the vapor pressure reached 4.5 mm. of mercury. As soon as it reaches 30 mm. the monohydrate takes up two more molecules and becomes the trihydrate; while at 47 mm. and above the trihydrate adds two more molecules and becomes the pentahydrate. Conversely, should the vapor pressure fall below 47 mm., the pentahydrate loses water and is transformed into the trihydrate, and so on. The constitution of the copper sulfate, in fact, precisely responds to the vapor pressure of water around it. Many like cases might be cited. The peculiarity of these is that while the external factor may change steadily, the physical response will be discontinuous. Among the multifarious phenomena of irritability in plants are some which are so nearly parallel to the behavior just described as to suggest an analogous causation.

It is possible that the application of the term irritability to the behavior of crystals will seem an unwise straining of its usual sense. Irritability has often been enumerated among the distinguishing properties of protoplasm. Even Sachs wrote:

Irritability is the great distinguishing characteristic of living organisms; the dead organism is dead simply because it has lost its irritability.

But if we are to consider irritability as a property— a characteristic—of protoplasm, it must be understood to be a conditional property, as strictly limited by circumstances as are the properties of non-living matter. Steel may be highly tenacious at certain temperatures; but at the temperature of liquid air it is as brittle as glass and can be pulverized by a blow. A frond of *Laminaria* when wet is a tough flexible strap, but when dry it is so rigid and brittle that it can be broken to fragments by slight bending. Many a plant is clearly irritable at moderate temperatures when well watered and lighted, but loses its irritability completely under adverse conditions. Becquerel has dried seeds for six months in a vacuum with barium hydroxid at 40°, sealed them for a year in a glass tube exhausted to 0.002 mm. of mer-

cury, kept them in liquid air at a temperature of — 190°
for three weeks and in liquid hydrogen (— 250°) for
three days. Is it possible to conceive of irritability ex-
isting under such conditions? Is it, indeed, possible to
conceive of life as latent? I think not. Irritability must
be counted as completely lost during this time, and as
regained when the seeds germinated, as they did when
suitable conditions were furnished. To emphasize the
conditional nature of this quality, it may be better to
describe protoplasm when irritable as in a state or con-
dition, instead of following the example of the physicist
in saying that it possesses the property of irritability,
of which it may be as surely dispossessed as steel may be
of its tenacity.

Of recent years Bose has the merit of having insisted
upon the essential similarity of response in living and
in non-living matter. His ''Plant Response'' and ''Com-
parative Electro-physiology'' are based upon this con-
ception; and though they contain much that can not be
approved, I am in complete accord with the thesis that
plants are intelligible only as mechanisms whose be-
havior, though more complicated than that of non-living
systems, is to be described by analogous laws.

While recognizing the essential unity manifest in the
behavior of all matter, we must nevertheless discriminate
between physical and physiological response. It is not
possible, however, to use these terms as they have been
used, even by Bose, to designate, respectively, the re-
sponse of non-living and living matter, since many of the
responses of organisms are purely physical. Physical
response, as I conceive it, is marked by the fact that the
energy applied to the body is a full measure of the effect
produced. Thus, when the conductivity of a selenium
plate is altered by light, the molecular disturbance (if
we so explain it) is initiated by the radiant energy, and
the effect is precisely measured by the energy applied
from the outside. The selenium contributes nothing. It
is acted upon, and its condition is altered for the time

being, by the external agent. The effect dies out shortly
after the agent ceases to act. Whether there is a loss of
energy or a gain, no further change ensues in the system,
unless it is acted upon from the outside.

Physiological response, on the other hand, though at
bottom of the same sort, differs in that the external agent
produces an upset that releases energy previously ac-
cumulated, so that the effect exceeds that due to the ini-
tial energy acting upon the organism. That is why, in-
deed, the term *stimulus* was originally applied to such an
agent; it brings into action energy often vastly greater
than its own. In this case there is a run-down of energy.
The system contains less than before by as much work as
has been done in response to the stimulus. Repeated
responses lead to exhaustion of the accumulated energy,
when further stimulation is impotent. To explain such a
situation Bose's theory of molecular strain is inadequate;
we are driven to take account of stored energy, and not
a direct supply. For if the depleted system be kept
under conditions as nearly uniform as possible, it pro-
ceeds to recover energy by the incorporation of new ma-
terial with its potential energy. The protoplast assimi-
lates food and presently is ready for new response to any
stimulus. It is the cyclic character of their energetics
that characterizes living things, no less in the phenomena
of response than in nutrition.

Even a casual examination of the various responses of
an organism shows clearly that some of them are to be
classed with the physical and others with the physiolog-
ical, as above defined. If so, it is plain that it is not mere
responsiveness that marks living things, for non-living
matter responds; it is the ability after a loss of energy
by response to regain, by the aid of the environment, a
condition which makes response possible once more.
This is no mere restoration of a molecular equilibrium
which has been disturbed or relief from molecular strain;
it involves acquisition of energy. How far this is due to
a direct intake of energy and how far to the utilization of
potential energy in available foods, our present knowl-

edge of the energetics of plants does not enable us to decide. Certainly we can not accept the source proposed by Bose, when he writes:

And now we see that the fine ramifications of fibrovascular elements over as wide an area as possible in the leaf provides a virtual catchment basin for the reception of stimulus. The expanded lamina is thus not merely a specialized structure for the purpose of photosynthesis, but also a sensitive area for the absorption of stimulus, the effect of which is gathered into larger and larger nerve trunks in the course of its transmission downwards into the body of the plant.

It is of course possible to use the term *stimulus* to designate any external or internal agent that produces an effect upon the organism, and *response* for the effect produced; but that use of the terms tends to confusion. Yet, besides the erratic treatises of Bose, some recent text-books use the words in this way. One, for example, reads: "Responses to water stimuli.—The primary responses of the plant to the water of the habitat are four: namely, absorption, diffusion, transport, and transpiration." It is hardly necessary to point out that if such processes are responses, then every change that occurs in nature is a response and every agent a stimulus. By such a usage we should lose the whole value of the discrimination embodied in the terms.

The less clearly plant processes are conditioned by the environment, the more likely they are to be reckoned responses to stimuli. Growth, for example, is often considered a response to stimuli; but it seems most likely that it is quantitatively determined by various factors (turgor, temperature, oxygen, food, etc.), any one of which may limit it. Stimulation by gravity or light may be an added factor, interlocking with one or more of them, and, by inducing local variation in the rate of growth, producing curvature; which is obviously a physiological response, for when the effect of the stimulus passes away the ordinary rate may be resumed.

In considering the energetics of response, it is essential not to forget that many stimuli *inhibit* actions going on at the time excitation occurs. There are many familiar examples of this among animals, but few in plants.

One well known is the interference of stimuli in tendrils. As Fitting showed, friction on the dorsal side of tendrils which usually curve after irritation of the ventral side, inhibits the curvature, not by setting up a countervailing rate of growth, for it apparently has no power to influence growth, but by interfering with the reaction somewhere between perception and the growth response. Here, if the stimulus were a source of energy, or limited the reaction, the double excitation should produce a doubly strong response. Nor can the well-known interference of light or sound waves in unlike phases be cited as an analogy of the inhibition in this case, because no such superposition is possible. It must be admitted that in cases of this kind the energy of the stimulus is not directly related to the response.

Of course, in urging this I must not be understood as denying that the excitation is often proportional to the intensity and duration of the stimulus, and that the final response may be influenced by the amount of excitation; the point is only that potential energy is released in amounts not at present referable quantitatively to that of the stimulus.

On analyzing the varied reactions to stimuli, it will be found in many cases that it is possible to recognize two well-marked phases, which may be designated *primary* and *secondary.* In other cases no such distinction can be made. One of the primary phases of response is known as *perception,* a word which, as used by plant physiologists, is entirely without psychological implications. Whatever change in the protoplasm is connoted by that term takes place almost instantly, as shown by the phenomena of summation. Stimuli of extremely brief duration—say a small fraction of a second—so transient that they produce no observable effect, nevertheless, if repeated at proper intervals, finally give rise to a reaction. The brevity of each period of stimulation gives indication of the speed of the perception change; for if no effect were produced by a single stimulus, repetition could have no effect.

Another primary phase of response is the propagation of the excitation. The disturbance called perception propagates itself, that is, it initiates in adjacent material a corresponding change, progressing from point to point, as shown by secondary effects produced at a greater or less distance from the point where the stimulus is applied. The precise character of the change itself has been little studied in plants, though the rate of propagation is known to be of the same order of magnitude as that in the nerves of the lower animals—say 1 to 10 mm. per second.

The secondary phase of response is manifested either separately by turgor mechanisms and by growth mechanisms, or by the two conjointly. In turgor mechanisms altered turgor of the cells in a definite region causes displacement of parts attached. In growth mechanisms local differences in the rate of growth of the organ displaces the adjacent parts. When combined the earliest displacement is due to turgor, and this is made permanent by growth.

Examples are so familiar that they need hardly be cited, and a single one of each will suffice. When the tip of a leaflet of *Mimosa* is stimulated by burning with a lens, the excitation is propagated to the petiolule of the leaflet, the turgor of its upper and anterior cells is so reduced that those on the opposite side compress them, bending the petiolule sharply and so carrying the leaflet forward and upward. The disturbance may spread to other leaflets and even to the base of the petiole, with appropriate curvatures in each motor organ.

When a primary root is placed horizontal, perception occurs mainly in the tip, the excitation is propagated backward, and the secondary response appears as differential growth of the cells chiefly in the third and fourth millimeter from the tip, which produces the well-known curvature.

Though much discussed, it is not clear whether the secondary response of tendrils depends on a growth mechanism or a turgor mechanism. I am inclined to be-

lieve that there is here a combination, the first curvature being due to a turgor change, which is fixed with unusual promptness by growth.

The movements of minute motile organisms, whether autonomous or induced, can hardly be analyzed, so intimate are the relations of the primary and secondary phases of response, if indeed they are separable.

All physiological responses when analyzed show the same general relations, no matter how varied the stimuli and the end reactions. If there were nothing more than the general applicability of Weber's law, this would be enough to suggest that there is some fundamental unity in the responses. There are, however, many other features that point in the same direction. It is obvious that the common factor is not to be found in the later phases of the response, where the structure of the organ may play a determinative rôle; nor in the direction from which the stimulus acts, which is known to determine often the direction of movement. Bose has sought to show that all cells when stimulated exhibit two concomitant responses, by which, it seems, he would account for all the phenomena of plant life, even to the ascent of water! Without assenting to his applications of the observations, we must say that Bose has done good service in showing that a mechanical contraction follows stimulation, and that change in electric potential occurs simultaneously. This, I think, we may consider established for a large number of plants, and it is very likely true of all. A study of the negative electric variation leaves us quite in the dark as to its significance, and though we are constantly tempted by electric analogies in the description of nervous phenomena, we gain no real insight yet into the rôle of electric stresses in organisms, because our knowledge of their causation is too vague.

In concomitant contraction and electric variation we have a two-phase phenomenon, which should be capable of further analysis. Is there any simpler action—more fundamental—which may produce both? To this question the recent work of Lepeschkin and Tröndle, supple-

menting earlier investigations, suggests an answer. Turgor variations have long been studied, but a reason for them has been sought in vain. We now know that various agents change the permeability of the protoplast to solutes, and that this sensitiveness is not limited to the specialized cells of a gland or a motor organ, but characterizes even the mesophyll. That this behavior occurs where there is no obvious relation to the functions of the organ, suggests at once that it inheres in the protoplast as a fundamental quality, in virtue of its chemical constitution or its molecular structure. It is perfectly easy to understand that this structure may be modified by the radiant energy already known to alter the permeability of the protoplast; and many other stimuli are of a kind to influence the unstable chemical compounds that compose protoplasm. If that estimate be verified by further researches, we shall be justified in considering *variability in permeability* as a basic property of protoplasts.

It will be evident enough that a change in permeability will permit the escape of some of the cell sap, with consequent shrinkage of the protoplast, stretched as it is by osmotic pressure, so that Bose's contraction would naturally result. Whether the escape of the solutes would account for the negative electric variation, I do not pretend to say, for the present theories as to electromotive force do not afford any light on the situation. Therefore, until the relation of electric stresses to other phenomena is better known, we must leave this question in abeyance.

The primary and secondary phases of a response may be understood readily in conformity to this conception. The sufficient stimulus or the summated excitation changes the constitution of the protoplast, and this change spreads along the protoplasmic lines of communication, until it reaches a region where the changed turgor results in a curvature, either directly, as in turgor mechanisms, or indirectly, by altering the rate of growth, as in growth mechanisms. That the turgor changes reported in the root undergoing geotropic curvature apparently do not harmonize with this theory is probably due

to the untimeliness of the observations. It is said that when the curvature is taking place the turgor of the cells on the concave side is unchanged and on the convex side lowered. But by the time curvature is well under way, the turgor conditions immediately following excitation may have undergone complete alteration, if we may judge from similar changes in motor organs. Thus, the original turgor, lowered on excitation (according to theory) by the increased permeability of the under side, may have been regained, while the very growth itself of the convex side may be responsible for the reduced turgor then observed on that side.

The responses of recoil and orientation in motile organisms are easily interpretable in terms of this conception, and though the application is purely hypothetical, it is no more so than the current explanations. Just such a change as results in changed permeability of the walled protoplast to solutes of the great vacuoles might take place on the passage of a naked protoplast into or out of a stimulation zone. How such a change can reverse the mechanism of movement is not explicable at present; but the new conception introduces no new difficulty. For example: If a change in surface tension is predicated as the result of excitation and the occasion of recoil, it is just through some change in chemical constitution that such an alteration in surface tension might come about. If the organism be one which orients itself to one-sided stimuli, orientation may as easily result from a local change in constitution as in any of the ways assumed by current theory.

No one is more keenly aware than I that these all are matters of speculation. They are presented as such. My hope is that they will direct attention to this phase of plant behavior and will stimulate thought, which should first clarify our conceptions, and then suggest lines of research.